UPPER PENNSYLVANIAN VERTEBRATES FROM THE SANGRE DE CRISTO FORMATION OF CENTRAL COLORADO

By Peter Paul Vaughn[1]

Abstract: On the basis of fragmentary vertebrate fossils found at a site low in the Sangre de Cristo Formation in the Arkansas River valley of Colorado, Brill (1952) tentatively assessed the age of this formation—in Colorado—as Early Permian and postulated a pre-Wolfcampian truncation of Upper Pennsylvanian strata in this region. Subsequent collection from Brill's site has produced many more disarticulated bones, as well as fragments of plants and shells of small pelecypods. Recognizable vertebrates include: palaeoniscoid fish, two or more kinds of labyrinthodont amphibians, a new genus and species of aistopod amphibian, a new species of the diadectid cotylosaur *Desmatodon,* an ophiacodont pelycosaur, probably a sphenacodont pelycosaur, and an edaphosaurian pelycosaur referable to *Edaphosaurus* aff. *E. raymondi.* The new aistopod has a mode of costal articulation that seems to be more primitive than that of known Pennsylvanian forms. Materials of the new species of *Desmatodon* greatly expand our knowledge of this hitherto poorly known genus and indicate greater primitiveness than seen in *D. hollandi,* described by Case in 1908 on the basis of a fragmentary jaw from the Conemaugh Series of the eastern United States. *Edaphosaurus* aff. *E. raymondi* corroborates approximate time-equivalence with the Conemaugh Series. At least the lower part of the Sangre de Cristo Formation in central Colorado seems, therefore, to be of Missourian (Late Pennsylvanian) age. This is consonant with the position of the Sangre de Cristo Formation directly above rocks of Desmoinesian age in this region. This is the first known occurrence of North American Pennsylvanian tetrapods west of eastern Kansas, and it promises new insights into the geographic distribution of Early Permian vertebrates.

Introduction

In a stratigraphic study of the uppermost Paleozoic rocks deposited in the zeugogeosyncline of Colorado and northern New Mexico—the trough between the Late Paleozoic San Luis-Uncompahgre and Front Range highlands—Brill (1952:821) redefined the Sangre de Cristo Formation in the region of central Colorado "to include the Permo-Pennsylvanian strata that overlie the Whiskey Creek Pass limestone or its equivalent." That is, he excluded from this formation the underlying Veta Pass Limestone Member of earlier authors. In central Colorado, in the valley of the Arkansas River, the Sangre de Cristo Formation as redefined is about 8800 feet thick. Temporal relationships with

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the Sangre de Cristo as exposed in northern New Mexico have remained unclear. As Brill pointed out, near Pecos, New Mexico, the Sangre de Cristo overlies strata of Virgilian (latest Pennsylvanian) age and underlies strata of Leonardian (Early Permian) age and is probably a time-equivalent of the Abo Formation of central and southern New Mexico—which is Wolfcampian (earliest Permian) in age. Brill (1952:822) saw two possibilities for the Sangre de Cristo of the Arkansas River valley: "Either the lower part of the Sangre de Cristo formation in . . . Colorado is a nonmarine equivalent of the upper Pennsylvanian marine strata in northern New Mexico, or the Sangre de Cristo is mainly Wolfcamp and the upper Pennsylvanian has been truncated by a pre-Wolfcampian unconformity." Brill tentatively chose the latter as the correct explanation, on two lines of evidence: (1) the Sangre de Cristo of the Arkansas River valley rests on rocks of Desmoinesian (Middle Pennsylvanian) age, and (2) vertebrate fossils found low in the Sangre de Cristo of this region seemed to indicate Wolfcampian age. Nevertheless, he remained troubled by the lack of good lithologic evidence for a pre-Wolfcampian truncation, as shown by his remark (1952:842) that "nonmarine strata [of the zeugogeosyncline] assigned to the Wolfcamp may be upper Pennsylvanian entirely or in part." Baltz (1965:2054) expressed this same uncertainty when he referred to Brill's paper by saying: "Early Permian vertebrates have been found in the Sangre de Cristo Formation, but it has not been established whether the formation also contains rocks of Pennsylvanian age in Colorado."

In the course of a study of Early Permian vertebrates of the Four Corners area, I have re-examined the fossils noted by Brill, and I have made further collections at the site whence they came. Study of the fossils convinces me that Brill's first alternative is the correct one, that at least the lower part of the Sangre de Cristo Formation in central Colorado is a nonmarine equivalent of Upper Pennsylvanian marine strata in northern New Mexico. More specifically, these fossils seem to indicate Missourian age. Not only is this interesting from a stratigraphic point of view, but the fossils shed light on some problems in the understanding of Late Paleozoic vertebrates. Vertebrate-yielding Pennsylvanian deposits are rare anywhere in the United States, and this is particularly true of the West. The Sangre de Cristo site provides our first knowledge of Pennsylvanian tetrapods west of the now well known Garnett quarry of eastern Kansas (see Peabody, 1952). Further, the fossils from the Sangre de Cristo greatly supplement previously meager data on the Pennsylvanian diadectid cotylosaur *Desmatodon,* and they provide amplification of our knowledge of the aistopod amphibians.

The Fossils in General

Brill noted bones of cotylosaurian and pelycosaurian reptiles found in Interval 300 of his measured section of the Sangre de Cristo Formation near Howard, in Fremont County, Colorado. There is some slight discrepancy

within his paper as to the distance of Interval 300 above the base of the Sangre de Cristo, but his detailed section and a statement on page 834 of his paper make it clear that it is about 1450 feet. Following his directions to the fossiliferous bed, my crew and I found it in NE¼ SW¼ sec. 22, T 49 N, R 10 E, where it is cut by Rock Creek, a branch of Badger Creek, which latter drains into the Arkansas River about a mile and a half to the south. Brill's Interval 300 is described in his detailed section (1952:870) as "Shale dark red below, greenish gray . . . above, silty; basal bed darker, wedges out to north; a few thin beds of dark-gray limestone; shale contains ganoid fish scales, bones of *Diadectes* sp., and pelycosaurs." Interval 300 is about eight feet thick. The bones come from the dark, almost black, basal bed, which is about two to three feet thick at its deepest part—where it is cut by Rock Creek—and wedges out about 80 feet to the northwest. Most of the bones come from about 1.5 feet above the two-foot sandstone of Interval 299. On the southeast side of the creek, Interval 300 is covered by soil and vegetation.

The fossils collected by Brill are catalogued in the collections of the United States National Museum as USNM 18602, which consists of part of a vertebral neural arch definitely of a diadectid cotylosaur, the glenoid portion of a probably diadectid pectoral girdle, a vertebral centrum possibly from the caudal region of a diadectid, part of a vertebra of a small pelycosaur, a small piece of dermal bone of a labyrinthodont amphibian, a scale of a palaeoniscoid fish, and several other, small scraps of bone. The diadectid remains were identified as pertaining to *Diadectes,* a characteristic member of faunal assemblages known from Lower Permian rocks of north-central Texas, northern New Mexico and southeastern Utah (see Romer, 1960 and Vaughn, 1964), and never, as far as is known, found in the Pennsylvanian. It was on the basis of this identification that Brill assigned the Sangre de Cristo Formation of central Colorado to the Wolfcamp.

In the summers of 1966 and 1967, my crew and I excavated many more fossils from Brill's site in Interval 300. Large blocks of matrix and bone were removed to be prepared in the laboratory, where we found that—except for some aistopod vertebrae and osteoderms, and some palatal and anterior limb elements of a small labyrinthodont amphibian—no elements were in even partial articulation with one another although they lay close together. The bones are all quite dark, and often difficult to distinguish from matrix in the field; but many of them are excellently preserved although fragile, and can be associated as elements belonging to a number of species on morphological grounds even though in most instances it is impossible to relate them with certainty as parts of the same individual animal.

Besides bones, poorly preserved fragments of plants were found, as were also shells of small pelecypods. Because of the disarticulated nature of the remains, it has not been possible to identify all the vertebrates represented, but the following forms may be recognized: a palaeoniscoid fish; of labyrinthodont

amphibians, one small and at least one large rhachitome; of lepospondylous amphibians, a new genus and species of aistopod; of cotylosaurian reptiles, a new species of the diadectid genus *Desmatodon*; and of pelycosaurian reptiles, one ophiacodont, probably one sphenacodont, and an edaphosaur referable to *Edaphosaurus* aff. *E. raymondi*. It is *Desmatodon* that was mistaken for *Diadectes*. The aistopod, the edaphosaur and, especially, the new species of *Desmatodon* form the principal bases for re-assessment of the age of at least the lower part of the Sangre de Cristo Formation in Colorado as Late Pennsylvanian rather than Early Permian.

Abbreviations

The following abbreviations are used throughout the text to refer to repositories of specimens: AMNH, American Museum of Natural History, New York; CM, Carnegie Museum, Pittsburgh; FM, Field Museum, Chicago; UCLA, University of California, Los Angeles; USNM, United States National Museum, Washington.

Palaeoniscoid Fish

Palaeoniscoid fish are represented by a number of smooth, shiny scales with a diamond-shaped outline and with bevelled edges by which they articulated with adjacent scales. The largest of these scales are about 3.5 mm long (between acute apices) and about 2.5 mm wide (between obtuse apices). These scales and the small pelecypods, as well as the lenticular shape of the fossiliferous bed, offer evidence for aquatic origin of the deposit.

Labyrinthodont Amphibians

At least two kinds of labyrinthodont amphibians are distinguishable among the materials from Interval 300, one small rhachitome and one large one, and isolated teeth may represent a third kind.

The small rhachitome is represented by UCLA VP 1698, which consists mostly of partially articulated palatal elements but also includes part of a maxilla with teeth, a few fragments of an anterior limb, and perhaps some vertebral parts. There is also a partial impression of a lower jaw, and a small fragment of roofing bone that shows a pattern of fine pitting. About a dozen teeth can be seen on the fragment of maxilla, but only a few are complete. They are narrow cones with longitudinal grooves in their basal halves; the largest is 1.5 mm long. Of the few palatal elements present, the pterygoids are the best preserved, although twisted out of their natural positions with respect to one another, and there is also a displaced denticulate element that seems to be from the lateral palatal series. The left pterygoid is the more complete; it was about 20 mm long from near the posterior end of the quadrate process to where it met the vomer. To judge from proportions in a primitive rhachitome

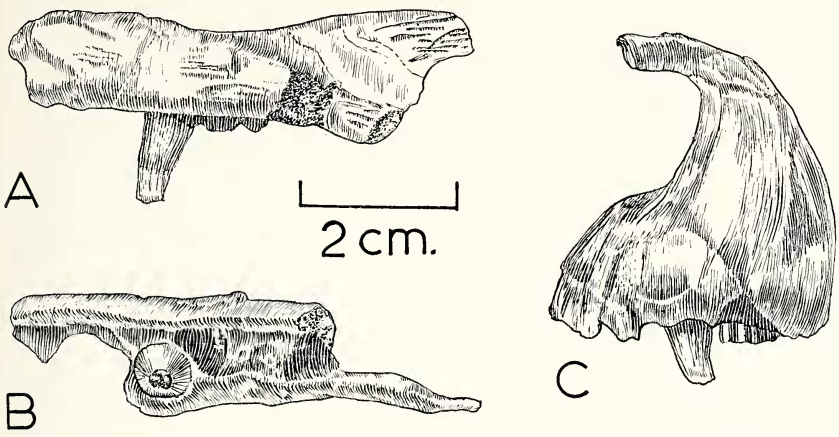

Figure 1. A, medial, and B, ventral views of the right palatine bone of a labyrinthodont amphibian, UCLA VP 1699. C, lateral view of the right premaxillary bone (and a bit of the right nasal bone) of a labyrinthodont amphibian, UCLA VP 1700.

such as *Dendrerpeton* (Carroll, 1967), the total length of the skull may have been about 30 mm. The pterygoids are finely denticulate in their anterior parts, and each shows a deep, posteromedially facing socket for the basipterygoid process of the braincase—the palate must have been mobile. Bowing of the medial edge of the palatine ramus of the pterygoid indicates fairly wide interpterygoid vacuities. Behind the palate lie some bits of shoulder girdle and free limb, but these permit no more than the observation that the limbs seem to have been relatively small. Posterior to this are fragments of which some may be pieces of thin-walled intercentra. The grooves in the teeth make it clear that this is a labyrinthodont amphibian; the mobile palatal articulation and the fairly wide interpterygoid vacuities would make it seem that we are dealing with an edopoid rhachitome, perhaps a dendrerpetontid. In the lack of more materials, it is not possible to be more definite.

UCLA VP 1699 (Fig. 1, A, B) is a tusk-bearing right palatine bone of a large rhachitome. The posterior part of the dentigerous portion is missing, but the maxillary process seems to be almost complete and this allows an estimate of total length, from where the palatine met the vomer to its junction with the ectopterygoid: about 65 mm. The maxillary process extends dorsally and posteriorly as a stout blade with a roughly scored lateral surface—it is difficult to find illustrations of the maxillary process, but Bystrow (1939) shows it in the Lower Triassic capitosaurid *Benthosuchus*. There is a smooth, posteriorly sloped shelf on the dorsal surface of the dentigerous portion medial to the maxillary process. The narial surface is well preserved; the vomerine process of the palatine bounded the choana medially, and the dentigerous portion bounded it posteriorly. One tusk is preserved but the tip is missing; what

remains is 11.5 mm long. The tusk is circular in section near the tip and almost circular, with a diameter of 6.0 mm, at the expanded base. The proximal two-thirds or more of the tusk is fluted by numerous longitudinal grooves. There are three poorly defined empty sockets behind the preserved tusk and perhaps the remains of a crushed socket in front, and there were probably more in the lost posterior part; the sockets all lie within a groove with a thin lateral and a thick medial wall. The palatine is 13.7 mm wide in the plane of the preserved tusk and thins to 11.5 mm at the posteriormost preserved socket. The greatest height of the dentigerous portion of the palatine, near the anterior border of the preserved tusk, is 13.0 mm. The medial surface of the dentigerous portion of the palatine shows distinct grooves for articulation with the pterygoid. These grooves end anteriorly at about the plane of the preserved tusk, which indicates that there was a fairly well developed interpterygoid vacuity, that the palatine formed part of the lateral boundary of the vacuity, and that the pterygoid did not meet the vomer. The slimness of the palatine as seen in ventral view suggests a narrow snout.

A right premaxillary bone with two teeth, UCLA VP 1700 (Fig. 1, C) possibly belongs to the same amphibian whose palatine bone has just been described. A lightly "sculptured" bit of the nasal bone is attached to this premaxilla, but the suture is difficult to follow. The premaxilla is about 40 mm in length along the ventral margin and is about 15 mm thick from medial to lateral surface as measured at the anterior border of the naris. The bar in front of the narial opening is massive, about 22 mm from front to back at the ventral border of the naris. Below the naris, there is a thin, recessed sheet for the reception of the maxilla. Disturbingly, this sheet is separated on its medial side, by a smoothly walled concavity, from a smaller sheet that extends caudad from near the line of articulation of the premaxilla with its partner; the concavity may have formed the anterior portion of an anterior palatal vacuity—such openings are known in the narrow-snouted archegosaurid rhachitomes (see Romer, 1947) but in these they are wholly surrounded by the premaxillae. Should the concavity be part of a choana rather than a palatal vacuity, its proximity to the midline would suggest an embolomere rather than a rhachitome. Only the very base of the anterior premaxillary tooth is preserved in UCLA VP 1700, but this is enough to indicate an enormous tooth. The base is oval, 12.5 mm long from front to back but only 6.5 mm wide. The second tooth has a base 7.7 mm long and 5 mm wide. This second tooth is 10 mm long as preserved; the tip is lacking. The greater length of this tooth is fluted by coarse longitudinal grooves, but near the tip, where there is a slight bulbous expansion, the surface is smooth. When this premaxilla was first found, it was thought that it pertained to the new species of *Desmatodon* described in this paper, but this now seems unlikely. For one reason, the better preserved tooth in the premaxilla is similar to the tusk of the palatine bone described above—but this is not a cogent point because of the unreliability of comparisons be-

tween marginal and palatal teeth. A more compelling argument lies in the comparison of the premaxillary teeth with isolated diadectid "incisors" undoubtedly referable to *Desmatodon* from Interval 300. There are a half dozen of these incisors, and they look nothing like the teeth of UCLA VP 1700. The diadectid incisors (described more fully in a later section) have a fine longitudinal striation that contrasts sharply with the coarse fluting in UCLA VP 1700, and there is no sign in the latter of the excavation of one surface of the tooth to form the chisel-like crown that is so prominent a feature in the incisors of *Desmatodon*—and of *Diadectes*. Rather, the better preserved tooth of UCLA VP 1700 looks very much like certain other isolated teeth from Interval 300; in these, too, the fluting is coarse and there is a slight bulbous expansion proximal to the tip. In the isolated teeth the tip is strongly recurved —perhaps this was also true of the teeth of UCLA VP 1700. It is mostly on the basis of the teeth, then, that I think the premaxilla belongs to the labyrinthodont amphibian represented by the palatine bone, but it may also be noted that the shape of the premaxilla is such that the anterior end of the snout must have been quite narrow; this would fit the shape of the snout as postulated on the basis of the palatine.

The entrance of the palatine into the border of the interpterygoid vacuity indicates that this vacuity was fairly well developed, and this denotes a rhachitome. But what kind of rhachitome? A search through Romer's review of the labyrinthodonts (1947) has not allowed even tentative superfamilial identification. The best that can be said is that the structure of the palatine suggests some similarity to the narrow-snouted archegosaurids, but these rhachitomes are not known below the Permian.

A single neural arch (UCLA VP 1702) of rhachitomous aspect is appropriate in size to the palatine bone, as is a fragment of a squamosal bone from near the border of the otic notch. The squamosal has the typically labyrinthodont style of pitting on its external surface, and this may also be seen on other fragments of dermal bone from Interval 300.

Still other isolated labyrinthine teeth from Interval 300 indicate perhaps a third kind of labyrinthodont amphibian. The largest of these teeth is about 15 mm long. They are coarsely grooved, are oval in section near the base, and taper with continuous recurvature to a pointed tip.

Obviously, the nature of the labyrinthodont remains, and my misgivings as to the association of the premaxilla, do not permit the setting up of new taxa.

NEW GENUS AND SPECIES OF AISTOPOD AMPHIBIANS

Class AMPHIBIA

Subclass LEPOSPONDYLI

Order AISTOPODA

Family OPHIDERPETONTIDAE

Coloraderpeton, new genus

Type species: *Coloraderpeton brilli,* new species

Diagnosis: The vertebrae of *Coloraderpeton* differ from those of *Ophiderpeton*—the only other known genus of the Ophiderpetontidae—in that the neural spine, instead of being low and bladelike, is tall, has a crenulated dorsal edge, and does not extend the full length of the vertebra. The ends of the capitulum and "tuberculum" (costal process) of the rib, instead of being cupped, are condylar; and the posteromedial process of the rib is short and rounded, rather than long and pointed.

Coloraderpeton brilli, new species

Holotype: UCLA VP 1689, a dorsal vertebra (Fig. 2, A, B, C, D).

Referred specimens: UCLA VP 1690, proximal part of a rib, preserved portions slightly displaced along a fracture (Fig. 2, E); UCLA VP 1691, three partially articulated dorsal vertebrae, with many scattered, but some partially articulated, osteoderms on the same small piece of matrix; UCLA VP 1692, many disarticulated vertebrae and osteoderms.

Horizon and locality: The holotype and referred specimens were collected by a field party from the University of California, Los Angeles, in the summer of 1966, from Interval 300 of the section of the Sangre de Cristo Formation measured by Brill (1952:870), about 1450 feet above the base of the formation, in NE¼ SW¼ sec. 22, T 49 N, R 10 E, Fremont County, Colorado. The holotype and referred specimens were all found close together, within an area of about a square foot, some distance removed from other bones found at this site. The foramen for the spinal nerve in the vertebrae, the tetraradiate structure of the rib, and the fusiform shape of the osteoderms are all typically aistopod features that preclude any possibility of incorrect assignment. While it may be that all these specimens are parts of a single individual, this is uncertain—hence the designation of a single dorsal vertebra as the holotype. The age is Late Pennsylvanian, probably Missourian. The species is named in honor of Kenneth G. Brill, Jr., who discovered the site.

Diagnosis: The same as for the genus.

Description and discussion: Baird (1964) has published a survey of aistopod amphibians that has made distinction of *Coloraderpeton* an easy task. The Mississippian form he mentions has not yet been described, but he was able to summarize the features of all other aistopods. According to Baird (1964:6), all, including the members of the family Phlegethontiidae, have "Vertebrae with low, blade-like neural spines" that extend "the full length of the vertebra." Indeed, Baird includes this feature in his list of ordinal characters. In view of this, it is possible that the new genus may represent aistopods different enough to form a new family, but it is otherwise so like *Ophiderpeton* in general features that I feel it belongs in the Ophiderpetontidae—monotypic

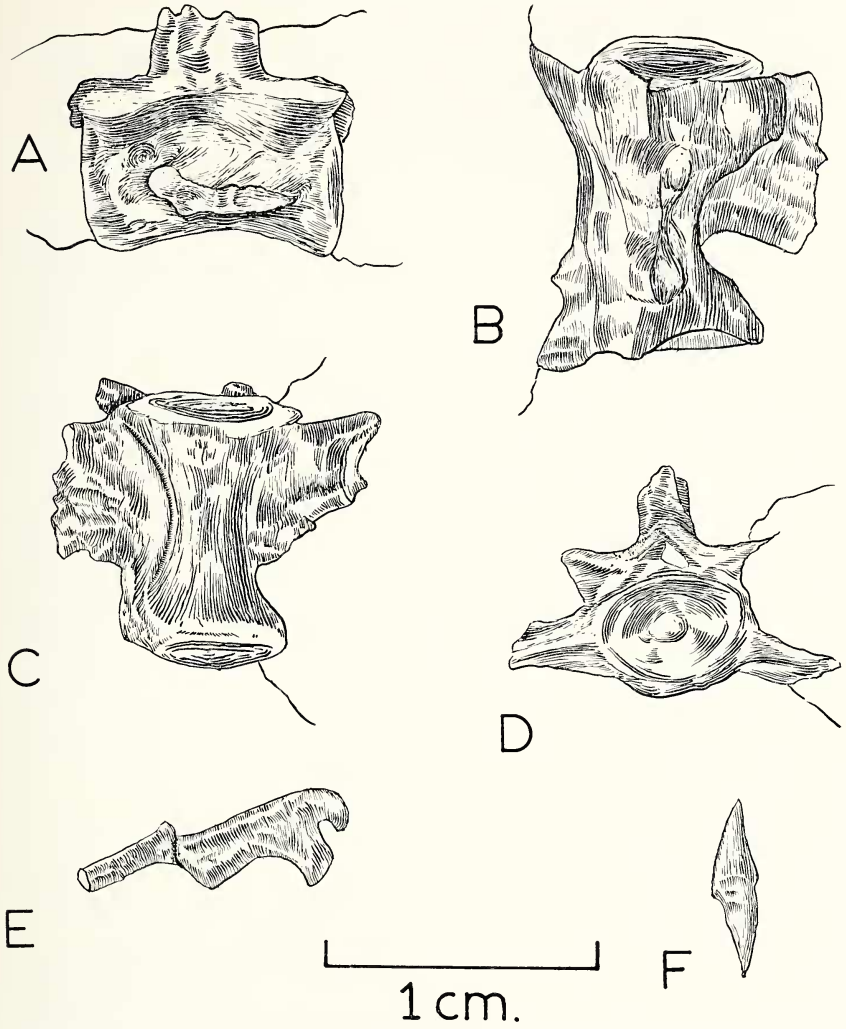

Figure 2. *Coloraderpeton brilli,* new genus and species: A, right lateral, B, dorsal, C, ventral, and D, anterior views of the holotypic vertebra, UCLA VP 1689; edges of adjacent matrix indicated by lines; in B and C, anterior is to the top. E, proximal part of a rib, UCLA VP 1690; note slight displacement along fracture. F, osteoderm.

up until now. In its similarities to *Ophiderpeton, Coloraderpeton* can be distinguished without difficulty from the Phlegethontiidae, a monotypic family, if *Dolichosoma* is, as Baird suspects, congeneric with *Phlegethontia.* Differences are immediately apparent: in *Phlegethontia,* the ribs have slender, flexible shafts and the posteromedial process is weakly developed at best,

whereas the shaft is stout in *Coloraderpeton* and the posteromedial process, although not long, is prominent; in *Phlegethontia,* the armor consists only of thin gastralia, whereas *C. brilli* has—as seen fairly well in UCLA VP 1691—the well developed "sheathing of fusiform osteoderms which are packed together in a herringbone pattern" that is characteristic of *Ophiderpeton* (Baird, 1964:8). An individual osteoderm of *C. brilli* is illustrated (Fig. 2, F); this osteoderm is 6.5 mm long.

Caudal vertebrae of *C. brilli* have not yet been recognized among the materials. The dorsal vertebrae are so like those of *Ophiderpeton* in general that only salient features need be discussed. The centrum of the holotypic vertebra (Fig. 2, A, B, C, D) is 8.7 mm long as measured along the ventral midline and has a transverse diameter of 6.0 mm at the anterior end; the lateralmost points of the transverse processes are 12.5 mm apart. The anteroposteriorly short, dorsoventrally tall, and dorsally crenulated neural spine is seen not only in the holotypic vertebra but also clearly in other vertebrae included among the referred specimens; there can be no doubt of this feature. As in *Ophiderpeton,* the neural canal forms a long tunnel the entire length of the vertebra. Baird (1964:6) noted that "In *Phlegethontia* a foramen for the spinal nerve occurs below the anterior end of the posterior zygapophysis or slightly further forward, behind the transverse process. This foramen appears to be present also in *Ophiderpeton* although it is generally obscured by dorsoventral compression or concealed by the dermal armor in the specimens at hand." The well preserved, uncrushed specimens of *C. brilli* would seem to confirm Baird's observation with regard to *Ophiderpeton;* all show the foramen—a useful identifying mark for aistopods. These foramina in *Coloraderpeton* are smaller than those in *Phlegethontia* as illustrated by McGinnis (1967).

Baird refers to the transverse process in aistopods as a parapophysis and says that it articulated with only the capitulum of the rib. This is undoubtedly the mode of articulation in *Phlegethontia,* but the matter is not as clear in the Ophiderpetontidae. In *Coloraderpeton,* at least, the articular surface of the parapophysis is divided into two distinct facets, which lie one in front of the other and are separated by a slight vertical ridge. Only one proximal part of a rib (UCLA VP 1690, Fig. 2, E) of *C. brilli* has been found, and this was not in natural articulation with a vertebra; but this rib can be easily fitted into the parapophysial facets in such a way that the "tuberculum"—better termed costal process as Baird says—articulates with the anterior facet and the capitulum articulates with the posterior facet, with the ridge between facets projecting into the angle between costal process and capitulum. It may be that *Coloraderpeton* differs in this way from *Ophiderpeton,* and perhaps the lesser development of the posteromedial process of the rib in *Coloraderpeton* is related to such difference; Baird notes that both costal process and capitulum have cupped heads in *Ophiderpeton,* but in *Coloraderpeton* the heads of both are condylar.

It is unfortunate that no cranial parts of *Coloraderpeton* have yet been recognized; nevertheless, what is known does supplement our knowledge of these too little understood limbless amphibians. The only aistopod found above the Pennsylvanian is a species of *Phlegethontia* known from the Lower Permian (McGinnis, 1967). Otherwise, the aistopods—including *Phlegethontia* —are a typically Carboniferous group. This in itself may support the argument developed more fully below, that at least the lower part of the Sangre de Cristo Formation in central Colorado is of Late Pennsylvanian age. There is additional support in apparent degree of primitiveness. In *Coloraderpeton* both the capitulum and the costal process of the rib are condylar, and both seem to have articulated with the vertebra; in *Ophiderpeton*, according to Baird (1964), both the capitulum and costal process are cupped, but only the capitulum articulated with the vertebra; in *Phlegethontia*, as may be seen in the illustrations published by McGinnis (1967), only the capitulum is cupped, and as she says, only the capitulum articulated with the vertebra. In this seeming sequence of decreasing emphasis on the costal process as an articular part, it would appear that *Coloraderpeton* has the most primitive aspect; this sequence would also be consonant with McGinnis's opinion that *Phlegethontia* is more advanced than *Ophiderpeton*.

NEW SPECIES OF THE DIADECTID COTYLOSAUR DESMATODON

Class REPTILIA
Subclass ANAPSIDA
Order COTYLOSAURIA
Family DIADECTIDAE
Genus **Desmatodon** Case, 1908
Desmatodon hesperis, new species

Holotype: UCLA VP 1706, a practically entire left maxillary bone, with complete dentition (Fig. 3, A, B, C, D).

Referred specimens: UCLA VP 1712, "incisor" tooth (Fig. 3, E, F); UCLA VP 1713, cheek tooth; UCLA VP 1710, left half of atlantal neural arch; UCLA VP 1707, dorsal vertebra (Fig. 4, A, B); USNM 18602, partial neural arch of dorsal vertebra; UCLA VP 1708 and 1709, two caudal vertebrae (Fig. 4, C, D); UCLA VP 1716, chevron bone; UCLA VP 1714, right humerus (Fig. 5, A, B, C, D); UCLA VP 1715, ungual phalanx; UCLA VP 1717, various elements including teeth, dorsal and caudal vertebrae, fragments of chevrons and limb bones, and phalangeal elements.

Horizon and locality: The holotype and some of the referred specimens were collected by a field party from the University of California, Los Angeles, in the summer of 1966; the rest of the referred specimens were collected in 1967. The site is in Interval 300 of the section of the Sangre de Cristo Formation measured by Brill (1952:870), about 1450 feet above the base of the

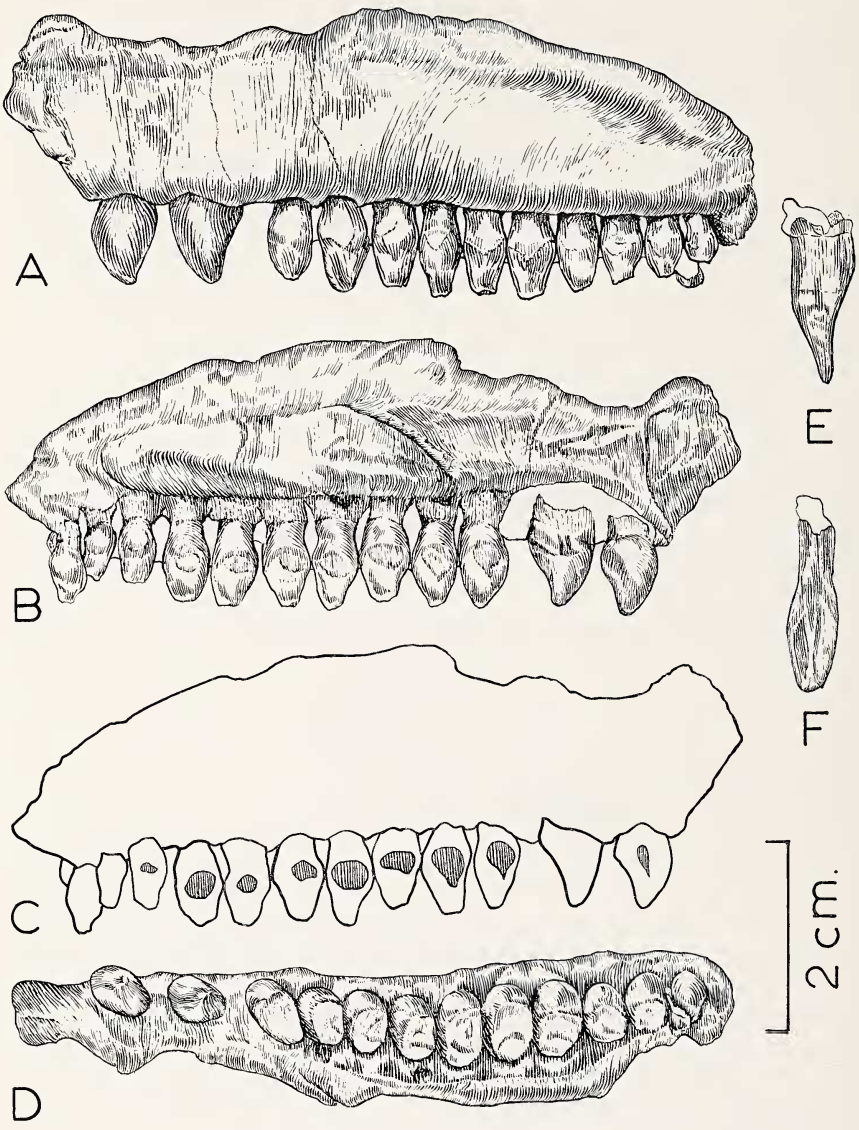

Figure 3. *Desmatodon hesperis,* new species: A, lateral, B, medial, and D, ventral views of the holotypic left maxillary bone and dentition, UCLA VP 1706; unshaded areas in A and B represent matrix; in D, anterior is to the left. C, outline sketch in medial view of the holotypic maxilla and dentition to indicate, by hachure, areas of attrition on teeth. E, lateral, and F, posterior views of an "incisor" tooth, UCLA VP 1712.

formation, in NE¼ SW¼ sec. 22, T 49 N, R 10 E, Fremont County, Colorado. None of the elements was articulated with another. Probably many of the specimens are from a single individual, but the fact that one cheek tooth (UCLA VP 1713) is significantly wider than any of the teeth in the holotype indicates that more than one individual is represented. The age is Late Pennsylvanian, probably Missourian.

Diagnosis: The maxillary bone and its dentition in *Desmatodon hesperis* may be contrasted with those in *D. hollandi,* the only other known species of the genus. In *D. hesperis* the ventral border of the lingual wall of the maxillary bone lies farther dorsally than does the ventral border of the labial wall, so that the bases of the teeth are more exposed on the lingual side; in *D. hollandi* the lingual and labial walls extend to about the same level. The central cusps of the teeth in *D. hesperis* are more prominent than in *D. hollandi,* but the lingual cusps are less well developed. The teeth in *D. hesperis* have crowns that are taller—measured on the labial side—than they are wide, whereas in *D. hollandi* the crowns are wider than they are tall. In *D. hesperis* the maxillary teeth—with the exception of the first and second—are set very close together; in *D. hollandi* each tooth is relatively shorter from anterior to posterior surface, and the space behind each tooth is equal to almost half the anteroposterior length of that tooth.

Description and discussion: Although the point is not crucial to this discussion, it may be appropriate at the outset to comment on my placement of diadectids as cotylosaurian reptiles—the classic classification. Romer (1964) has recently argued that the diadectids are better regarded as labyrinthodont amphibians closely allied to the seymouriamorphs. Although I have no doubt that the relationship to seymouriamorphs is close, many features of the diadectid skeleton indicate achievement of the reptilian structural grade. The matter is not settled, and I feel obliged to maintain a conservative position until more definite evidence of an amphibian life history is presented.

In 1908, E. C. Case described bones collected by P. E. Raymond at Pitcairn, about 15 miles east of Pittsburgh, Pennsylvania, at a level about midway in the Conemaugh Series. Case referred to the formation as the Pittsburgh Red Shale, but subsequently it has been called the Round Knob Formation (as in Romer and Price, 1940). From this site, Case noted remains of an eryopid rhachitome, an edaphosaurian pelycosaur, and a diadectid cotylosaur. The diadectid is represented by a fragment of a maxilla with four complete teeth and the root of a fifth, and by a number of chevron bones. Case designated the fragment of maxilla—CM 1938—as the holotype of *Desmatodon hollandi* and based the genus on this species. Case (1908:236-237) described the dentition as follows: "The teeth are transversely elongate; the crown is slightly wider than the root and is also somewhat swollen in the antero-posterior direction. The outer half of the crown rises gently into a sharp apex from which there is a sharp descent to the inner half, which is lower than the outer half. The inner

side of the apex is nearly vertical and presents a flat face inwards, this more prominent on the posterior and largest of the teeth than on the anterior ones. The surface of the crown is marked with fine lines and the sides of the root show the same character, but here the lines are coarser. The inner half of the crown of the anterior and the posterior teeth shows no wear, but on the two in the middle there are surfaces worn by attrition on both the inner half of the crown and on the apex."

Case noted the basic similarity of these teeth to those of the Lower Permian *Diadectes* and regarded the dentition of *Desmatodon* as more primitive. Romer (1952:86) elaborated on this comparison: "The *Desmatodon* teeth . . . appear to be built on the fundamental *Diadectes* pattern, but are far more archaic than in *Diadectes;* the most highly developed *Desmatodon* teeth are comparable to the least developed molars of *Diadectes*—those at the front or back ends of the 'molar' batteries. *Desmatodon* may well be, as its stratigraphic position suggests, a direct ancestor of *Diadectes*." Case illustrated the holotype (1908, Pl. 59, fig. 1) with the teeth pointing upwards and repeated this illustration soon afterwards (1911), although comparison with *Diadectes* would make it seem that his description was of upper teeth. Romer (1952:86), in a restudy of the holotype, said that "Diadectid 'molar' teeth show a pattern reversed in upper and lower jaws; in the upper teeth the major cusp is lateral in position, in the lower teeth, medial. Since Case refers to the major cusp in *Desmatodon* as lateral, it is obvious that he considered the specimen as pertaining to the upper jaw. Although this is uncertain (not improbably the specimen is the anterior portion of the tooth battery of the left dentary), we retain his orientation." Romer is quite correct in his description of the lateral placement of the major (central) cusp in the upper teeth of diadectids, but it is not at all clear that Case thought that CM 1938 was from the upper jaw—and it is not from a dentary. In a description of the dentition in *Diadectes,* Case (1911: 70) said that "The wear of the teeth produced flat faces on the inner cusps of the lower teeth and in advanced stages a deep triangular groove on the inner side of the medial cusp. The same effect was produced on the outer half of the upper teeth."

Not only is this the exact reverse of the pattern of attrition that I have observed in *Diadectes* dentitions at various museums (e.g., AMNH 4349 and FM UC 675), but it is even contradictory to the evidence presented by Case himself in a figure (1911, Pl. 1, fig. 6) of the right maxilla of AMNH 4349. As Romer (1952) has made clear, in the *upper* "molars" of diadectids the major cusp is lateral, and the attrition is concentrated on the inner (lingual) side. In the lower teeth, the attrition is concentrated on the labial side (see Welles, 1941). I have removed more of the recalcitrant matrix from CM 1938 and have exposed, near the base of one of the teeth, a pit of the kind called a "basal notch" by Welles (1941). These pits are found in *Diadectes* too, and they always lie on the lingual side of the teeth, in both upper and lower jaws. This

permits the positive statement that the major signs of attrition on the teeth in CM 1938 occur on the lingual side, and this identifies the holotype of *D. hollandi* as part of an upper jaw. Comparison with the holotype of *D. hesperis* makes it clear that CM 1938 is from the left side, but this can be adduced as well from a consideration of the relative positions of the labial and lingual edges of the maxillary teeth in *Diadectes.* In this form, as in *D. hesperis,* the greatest width of the tooth is not perfectly transverse; the labial edge lies somewhat anterior to the lingual edge. The teeth in *D. hollandi* are not perfectly transverse either; the angle of implantation indicates that the holotype is from the left maxilla, and this shows that Case was correct in his judgment that the larger teeth lie posterior to the smaller. That the holotype of *D. hollandi* is a fragment of the left maxilla is fortunate because it allows direct comparison with the holotype of *D. hesperis.* Except for differences in the amount of wear on individual teeth, the teeth of the holotype of *D. hesperis* fit the description given by Case for the teeth of *D. hollandi;* detailed distinctions are given above in the diagnosis of the former. Because *D. hollandi* is so poorly known, I prefer not to revise formally the generic diagnosis; obviously, it would include those features of the maxillary teeth that override the specific distinctions.

UCLA VP 1706, the holotype of *Desmatodon hesperis* (Fig. 3, A, B, C, D), is a left maxillary bone, 77 mm long, with twelve teeth. In *Diadectes,* as far as I have been able to learn from the literature and through personal examination of specimens, the number of maxillary teeth varies from eleven to thirteen with eleven the usual number. All the teeth except the most posterior one are excellently preserved; in the most posterior, the crown is fractured and the distal part displaced forwards. As in *Diadectes,* the maxilla has its greatest depth—19 mm in UCLA VP 1706—somewhat less than halfway back from the anterior end. Posterior to this, the gently convex dorsal border decreases gradually in height. Anteriorly, the thin lateral wall is broken along its dorsal rim, but it would appear that it did not decrease much in height. The external surface of the maxilla is bowed into a slight concavity; this surface is lightly rugose, but it is not "sculptured" as in labyrinthodonts. On the medial side, about 6 to 7 mm ventrad of the dorsal edge of the lateral wall, the maxilla thickens abruptly into a longitudinal bar that is convex dorsomedially. The greatest width of this bar, 15.5 mm, is in the plane between the eighth and ninth teeth; anterior to this the bar narrows slowly, but posteriorwards the narrowing is rapid. The part of the maxilla anterior to the first tooth is abruptly recessed to present an anteromedially facing concave surface that overlapped the premaxilla. This surface is continued posteriorly into a notch on the medial side of the bar above the first tooth. The lower border of the lateral surface of the maxilla extends farther ventrad than the lower border of the bar on the medial side, with the effect that the exposed part of the sixth tooth, for example, is only 8.5 mm long as measured on its labial side but 10.5 mm on the lingual side.

At the plane between the third and fourth teeth, a narrow channel begins just above the tooth row and passes posteriorly and dorsally across the medial and dorsal surfaces of the described bar to fade out at about the plane of the sixth tooth. Such a channel may be seen in *Diadectes* maxillae too (AMNH 4349 and FM UC 675 for examples), in which it also has its ventral end at about the plane between the third and fourth maxillary teeth. In *Diadectes* the ventral end of the channel lies immediately in front of the anteriormost part of the palatal process of the palatine bone. Olson (1947) thinks that the palatal process formed part of a secondary palate that was completed by a membrane. The similar placement of the channel in *Desmatodon* and *Diadectes* may indicate that a palatal process was present in the former too, although it was obviously not as tightly bound to the maxillary bone as in *Diadectes*—in which the two bones are practically inseparable. I cannot convince myself of the presence of the channel in the fragmentary maxilla of *D. hollandi,* although it may be represented by a poorly defined groove.

The general features of the maxillary teeth have already been noted in the diagnosis of *D. hesperis* and in the discussion of the holotype of *D. hollandi,* but some further description is required. As in *D. hollandi*—and also in *Diadectes*—the crowns of the teeth of UCLA VP 1706 are marked with light longitudinal striae; near the sockets the striation is coarser, and there seems to be a modified bone serving as cementum. Well developed basal notches are present on the lingual sides of the bases of at least the fourth and sixth teeth. As may be seen in the illustrations, there are marked gaps separating the bases of the first, second and third teeth. Posterior to these, adjacent teeth are set close together. The first two teeth are narrow from side to side and have a somewhat caniniform aspect: they are more acuminate than the succeeding teeth, they jut out slightly beyond the general tooth row, and their posterior edges are broadly concave and rather bladelike. The postero-lingual surfaces of the first two teeth are excavated in such a way that they approach the shape of the "incisors" described below. The third and fourth maxillary teeth are intermediate in structure between the first two and the more posterior teeth. The third overlaps the fourth on the lingual side, and to a lesser extent the fourth overlaps the fifth. The fifth through twelfth are readily recognizable as diadectid "molars" and resemble the teeth in the holotype of *D. hollandi* except for differences in proportions already noted. As in *D. hollandi,* the labial cusp is not the distinctly set off entity found in *Diadectes*; "shoulder" might be a better word than "cusp." The lingual cusp is more distinct, but far from as well developed as in *Diadectes.* As in *D. hollandi,* the lingual cusp does not extend quite as far distally as does the labial cusp. The central cusp in *D. hesperis* is longer than in *D. hollandi.* The difference in general aspect between the dentitions in the two species might be summed up by saying that the teeth in *D. hesperis* tend more toward an overall conical shape, and presumably this is more primitive than the condition in *D. hollandi.*

The crowns of the third through twelfth teeth in UCLA VP 1706 have their greater width in the transverse plane. They gradually increase in width from the third (6.6 mm wide) to the seventh, which has a width of 7.8 mm but a length from front to back surface of only 5.2 mm. The sixth through tenth are all almost as wide as the seventh, but the eleventh is only 5.8 mm wide and the twelfth is narrower than this, although measurement is difficult due to fracture.

The first, and the third through tenth teeth of UCLA VP 1706 show distinct wear facets on their lingual sides, on the lingual cusps in the teeth to which this term is appropriate (Fig. 3, C). Attrition on the lingual side is seen also in *D. hollandi* and is the pattern on the maxillary teeth in *Diadectes* too. Welles (1941) analyzed the motion of the lower jaw in *Diadectes* as propalinal and suggested that this animal, instead of being herbivorous as it is usually regarded, may have been molluscivorous. He based this suggestion partly on the abundant presence of thin-shelled pelecypods in association with certain remains of *Diadectes*. In this light, it is worth noting again that many small pelecypods were found along with the specimens of *D. hesperis* at the Interval 300 site.

It is difficult to determine the exact serial positions of the teeth in the holotype of *D. hollandi*. In comparison with the holotype of *D. hesperis*, they (including the tooth represented only by a root) could conceivably be the third through seventh, the fourth through eighth, or the fifth through ninth. The first two possibilities seem unlikely because of the lack of a clearly discernable channel on the medial side of the maxilla such as is seen in UCLA VP 1706, and also because of the degree of "molarization" of the first two teeth in CM 1938. It is likely that CM 1938 includes the fifth through eighth maxillary teeth and the root of the ninth. If this is so, then, unlike the condition in *D. hesperis* where the sixth through tenth teeth are almost equal in width, there would be a slight but steady increase in width from the sixth through ninth teeth in *D. hollandi*. The width of the eighth tooth in UCLA VP 1706 is 7.7 mm, and that of the probably corresponding tooth in CM 1938 is 9.5 mm—note also that the greatest width of the maxilla in this specimen is 18.7 mm as compared to 15.5 mm in the Sangre de Cristo maxilla. The teeth in *D. hollandi* are shorter from anterior to posterior surface—for the probably eighth tooth in CM 1938 this distance is 4.2 mm, and the corresponding measurement for the eighth tooth in UCLA VP 1706 is 5.3 mm—but the total length taken up in the maxilla by the five teeth is the same in both forms, due to the greater distance between successive teeth in *D. hollandi*. Details of these comparisons must, of course, be regarded with caution because of the uncertainty in determination of the serial positions of the teeth of CM 1938.

An isolated distal part of the crown of a cheek tooth from Interval 300, UCLA VP 1713, is conspicuously wider—10.5 mm—than the widest tooth in the holotype of *D. hesperis*. It is difficult to be sure which jaw the crown is

from, but the wear facet is on the shoulder that reaches slightly farther distally —the reverse of the condition in the maxilla—and this may indicate a lower tooth. It is not impossible to imagine that the lower cheek teeth might have been significantly wider than the uppers within the same individual, but this seems unlikely. This isolated tooth serves as a caution that all the disarticulated diadectid remains from Interval 300 are probably not from the same individual.

Six isolated "incisor" teeth from Interval 300 are confidently referred to *D. hesperis* on the basis of their great similarity to premaxillary and anterior dentary teeth in *Diadectes*. The longest and best preserved of these, UCLA VP 1712, is illustrated (Fig. 3, E, F). The root is lacking, but almost all of the crown seems to be present, and this is about 18 mm long. The fine longitudinal striation found in the "molars" is seen here too. The distal two-thirds of the posterior surface is broadly and concavely excavated so that the tooth is chisel-shaped in lateral view, and the distal half is gently expanded from side to side so that the tooth looks spadelike in posterior view. These incisors provide further confirmation of the correct assignment of *Desmatodon* to the Diadectidae.

The left half of an atlantal neural arch, UCLA VP 1710, from Interval 300, is similar to that of FM UR 27, a specimen of *Diadectes sideropelicus* from the Wichita Group of north-central Texas, although it is only about two-thirds as large.

Two almost complete diadectid dorsal vertebrae were found at Interval 300, and there are fragments of others; the most complete, UCLA VP 1707, is illustrated (Fig. 4, A, B), and it will be seen that this specimen has suffered some crushing. Perhaps the best way to characterize these vertebrae is to say that, had they been found as isolated elements in a Lower Permian deposit, they would almost certainly have been referred to *Diadectes*—within which there is considerable variation in details of vertebral structure—and it was exactly this mistake in identification of the fragmentary neural arch included in USNM 18602 that led Brill (1952) to his assessment of the age of the Sangre de Cristo Formation in Colorado as Wolfcampian. UCLA VP 1707 is about 100 mm high from the bottom of the centrum to the top of the slim neural spine; the almost horizontal zygapophysial surfaces lie about 35 mm above the bottom of the centrum; the left posterior zygapophysial buttress is incomplete, but the distance between the lateral tips of the zygapophyses must have been about 65 mm. Measured on its posterior face, the centrum is 23 mm wide and 24 mm deep. The nature of the episphenes is not clear, but hyposphenes were present on the posterior surface above the neural canal. Their articular surfaces faced ventrolaterally; they were not twisted to face upwards as they do in some *Diadectes* vertebrae, but there are also many specimens of the Permian form that show the presumably more primitive condition seen here. As in *Diadectes,* the transverse processes are elongate ridges that pass anteroventrally from behind the anterior zygapophysis, and the neural

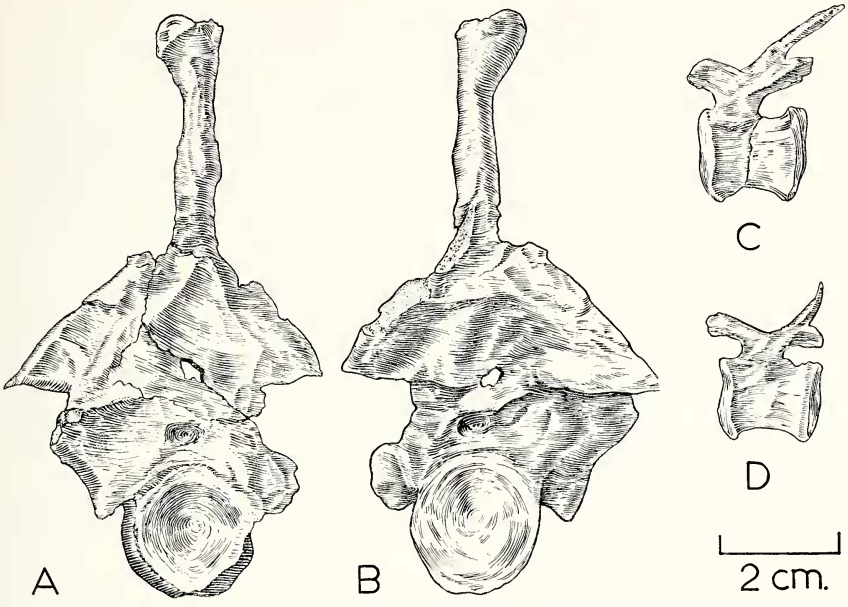

Figure 4. *Desmatodon hesperis*, new species: A, anterior, and B, posterior views of a dorsal vertebra, UCLA VP 1707. C, lateral view of a caudral vertebra, UCLA VP 1708. D, lateral view of a somewhat more posterior caudal vertebra, UCLA VP 1709.

spines are quadrangular in section with the angles directed fore, aft, and sideways. These vertebrae help demonstrate the truly diadectid nature of *Desmatodon*.

A number of caudal vertebrae from Interval 300 were at first difficult to identify, but I am now convinced that they are of *D. hesperis*. Two of these, UCLA VP 1708 and 1709, are illustrated (Fig. 4, C, D). The lack of transverse processes indicates that these are from well behind the region of the caudal ribs. The striking difference from *Diadectes* is in the slim neural spine, which slants strongly backwards, and which in at least some of the more anterior caudals—such as UCLA VP 1708—extended over part of the next posterior vertebra. In *Diadectes* (see Case, 1911 and Romer, 1944) the spine is stout and is directed almost straight upwards. Nevertheless, there is a compelling reason for recognition of these caudals as diadectid: traces of (much reduced) hyposphenes can be seen on the slight ridge beneath the almost conjoined posterior zygapophyses. The length of the centrum in UCLA VP 1708 is 17 mm, and in 1709 (from a more posterior position), 16 mm. These vertebrae are narrow in cross-section—the centrum in 1708 is only two-thirds as wide as it is tall—and the zygapophyses are set very close together. The

anterior zygapophysial surfaces face as much medially as they do dorsally. The ventral portion of the centrum is bevelled at both the anterior and posterior faces for the reception of the chevron bones. Actually, except for the slanted spines, these caudals are not unlike those in *Diadectes,* in which the zygapophysial surfaces are also inclined and in which the zygapophyses are set fairly close together—there is an abrupt decrease in the distance between contralateral zygapophyses within the length of the first sacral vertebra. Assuming that I have correctly identified the caudal vertebrae from Interval 300, the tail in *Desmatodon* must have resembled to a certain degree that in *Seymouria,* in which the neural spine also slanted backwards to cover part of the succeeding vertebra. White (1939) regarded the tail of *Seymouria* as a sign of a good swimmer. A similar condition of the neural spines may be seen in the obviously aquatic reptile *Mesosaurus*. Possibly then, there is some reason to believe that *Desmatodon* had somewhat more aquatic habits than did *Diadectes,* and it may be, but is not clear, that the more "fish-like" condition of the caudal neural spines in itself denotes greater primitiveness.

Two kinds of chevron bones were taken from Interval 300. One, represented by a single, incomplete specimen, is quite large and is probably of a labyrinthodont amphibian. The other kind is represented by an almost complete bone (UCLA VP 1716) and several fragments. These fit the description given by Case (1908) for diadectid chevrons found in association with the holotype of *D. hollandi.* The largest chevron described by Case is 51 mm long. UCLA VP 1716 is incomplete distally, but it appears to have been at least that long.

There are a number of partial ribs from Interval 300. Some of these seem to be appropriate in size to the dorsal vertebrae described above, but none has a complete head, and identification is uncertain.

Brill's (1952) collection from Interval 300, USNM 18602, includes a fragment from the glenoid region of a right scapulocoracoid that I identify, with some hesitation, as pertaining to *D. hesperis.* Part of the supraglenoid buttress is preserved, and this is pierced by the supraglenoid foramen—as in *Diadectes.* But not only is this condition common among cotylosaurs, it occurs in ophiacodont pelycosaurs too and, as I note in the next section, there are signs of a fairly large ophiacodont from Interval 300. Unfortunately, that part of the bone where there is a prominent process for the coracoid head of the triceps muscle in ophiacodonts is not preserved. What is present agrees with the illustrations of the *Diadectes* scapulocoracoid published by Case (1911). The glenoid facet is twisted into a somewhat screwlike shape and extends ventrally at its front end to overhang the area of the coracoid foramen. The anteroposterior length of the facet must have been about 45 mm, and this seems appropriate to the humerus described below.

UCLA VP 1714 (Fig. 5, A, B, C, D), a right humerus from Interval 300, has lost the deltopectoral crest and the posterior part of the head, as well as

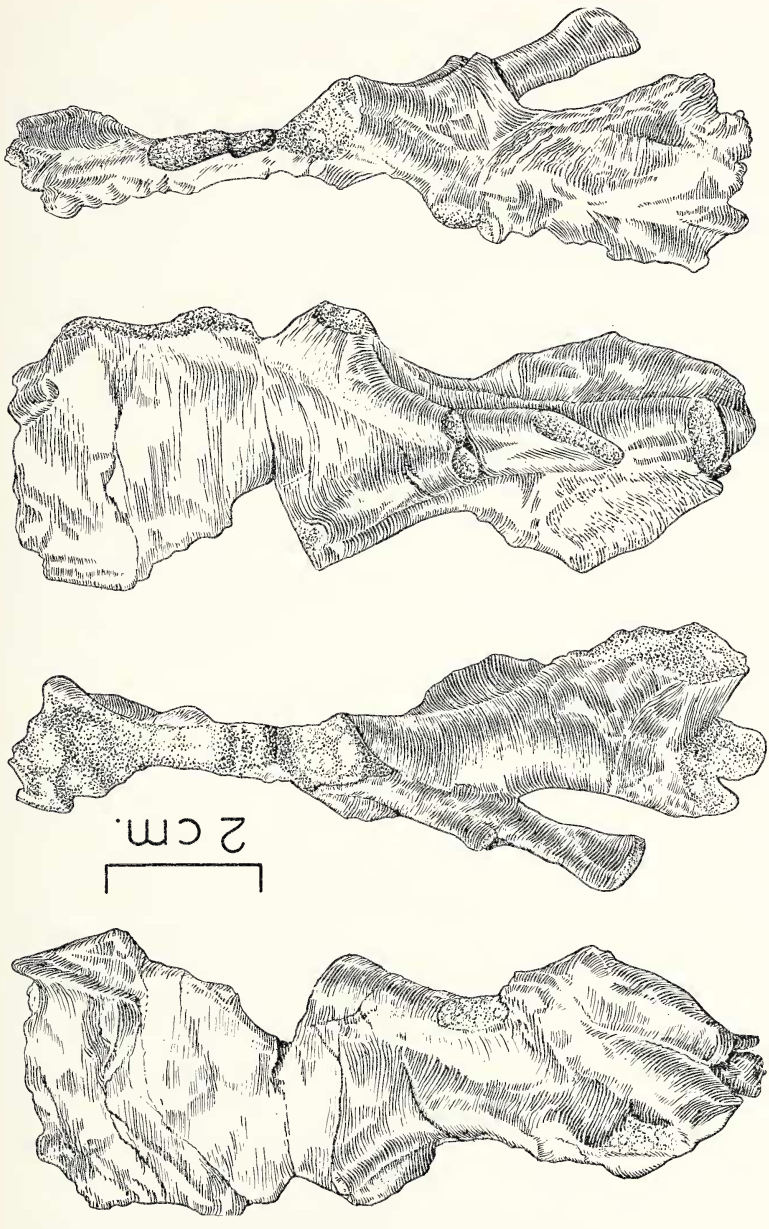

Figure 5. *Desmatodon hesperis,* new species: A, proximal-dorsal, B, distal-dorsal, C, proximal-ventral, and D, distal-ventral views of the right humerus, UCLA VP 1714.

most of the supinator process and the entepicondyle. Nevertheless, it may be assigned to *D. hesperis* with complete confidence. As in *Diadectes* (see Romer, 1956), the basic structure is tetrahedral, with the proximal surfaces set at a right angle to the distal surfaces; this is especially obvious in distal-dorsal and distal-ventral views (in the terminology of Romer). The total length of the humerus as preserved is 96 mm. A detailed description of UCLA VP 1714 would merely repeat the available descriptions of the humerus in *Diadectes;* only differences need be stressed. In general aspect, the humerus is somewhat slimmer than in *Diadectes.* This appearance is partly due to the fact that the anterior and posterior parts of the head and most of the supinator process were broken away, but it is nevertheless clear that there is in *D. hesperis* at least something of a shaft between the proximal and the distal parts of the element; in *Diadectes* the proximal and distal parts are, so to speak, simply turned on one another and a shaft is barely recognizable. The head has suffered the most crushing and is incomplete, but it seems not to have differed in any substantial way from *Diadectes.* The ectepicondyle is less prominent than in *Diadectes.* Much of the entepicondyle has been lost, and the outer bar of the entepicondylar foramen has been fractured at its proximal end and displaced towards the shaft, but what is left indicates that this region was similar to what is seen in *Diadectes.* In *D. hesperis* the base of the supinator process lies a little farther distally—nearer to the capitellum—than in *Diadectes,* probably in correlation with the more distinct shaft. What remains of the stump of the supinator process shows that it was more constricted at its base than in *Diadectes,* in which the base is broadly flared along a longitudinal plane.

Case (1911, Pl. 11, figs. 4, 5) illustrated a humerus, FM UC 6541, from the Conemaugh Series near Danville, Illinois. This humerus has had a complicated nomenclatorial history that I need not discuss, but lately it has been informally reputed to be diadectid, and it probably forms part of the basis for Romer's statement (1952:87) that "It is possible that a few fragments of bones of diadectid appearance from the vertebrate bonebed at Danville, Illinois, and of the same general late Pennsylvanian age, may pertain to *Desmatodon.*" Other fragments from Danville may indeed be diadectid, but I have examined the humerus and found that, except in characters common to very primitive cotylosaurs, it is not like that of *D. hesperis;* it much more likely has limnosceloid affinities, and Dr. R. L. Carroll, who has also examined this specimen, has written to tell me that this is also his opinion.

Four ungual phalanges from Interval 300 are obviously of *D. hesperis* because they are so completely like the unguals of *Diadectes* figured by Case, and they fit the description (Case, 1911:83) in being "broad and spatulate, with thin and very rugose edges. . . ." The largest of these, UCLA VP 1715, is 12 mm wide and 14 mm long.

There cannot be any doubt that *Desmatodon* is related to the Early Permian *Diadectes,* and it seems quite obvious on the basis of the dentition that

Desmatodon is much the more primitive genus—as Romer (1952) has already said. The other Early Permian diadectids, including *Diasparactus* and *Phanerosaurus,* are not as well known, but Romer (1956) feels that they form a compact group with *Diadectes* as apart from *Desmatodon.* Even without our knowledge of *D. hollandi,* the presence of specimens of *D. hesperis* in Interval 300 would argue strongly for Late Pennsylvanian, rather than Wolfcampian, age; but the remains of *D. hollandi* from the Conemaugh Series make this clear and indicate a position within the Missouri Series for at least the lower part of the Sangre de Cristo Formation in central Colorado. It has been noted above that the dentition in *D. hesperis* may be regarded as somewhat more primitive than that in *D. hollandi,* but this does not seem to be sufficient reason to postulate much greater age.

Romer (1964) has made clear his opinion that diadectids are closely related to the seymouriamorph labyrinthodont amphibians, and the recent description of the Lower Permian form *Tseajaia* (Vaughn, 1964), which seems in some ways to demonstrate a morphologically intermediate stage, supports this opinion, although it does not necessarily follow that diadectids must be regarded as amphibians rather than reptiles. The specimens described in this paper show that *Desmatodon* was similar to *Diadectes* not only basically but also in many details. The line leading to diadectids must have split away from the more general seymouriamorph stock at a time well before Conemaugh-Missouri deposition.

PELYCOSAURIAN REPTILES

In any collection from a quarry where many disarticulated and jumbled bones are found, it may be expected that some elements will be unidentifiable below the level of major taxonomic grouping. This is true of pelycosaurian elements from Interval 300. Assorted items, including teeth, fragments of jaws, and pointed claws, indicate the presence of several kinds of pelycosaurs, but except for the recognition of a few elements as ophiacodont, the probably correct identification of a toothed fragment of maxilla as sphenacodont, and the fairly detailed identification of an edaphosaur, these items must remain labelled simply "pelycosaurian" for the present.

A part of a neural arch—UCLA VP 1695—including the left posterior zygapophysis and the base of the spine seems quite clearly to be of an ophiacodont. What remains of the spine shows that it had the bladelike shape characteristic of ophiacodonts, and the neural arch is not laterally excavated as it is in sphenacodonts. The base of the spine, from anterior to posterior edge, is about 12.5 mm long; the greatest thickness of the spine is 3.0 mm.

Two partially preserved ilia, a right and left (UCLA VP 1696 and 1697), are also of ophiacodont aspect and are of a size that may be considered appropriate to the neural arch described. Measurements are hard to take on these specimens; the right one seems to have suffered some post-mortem flattening,

but the left is less altered and in this the neck of the ilium is about 34 mm from anteriormost to posteriormost point at the level of the supra-acetabular buttress. These ilia look similar to those of the Lower Permian *Ophiacodon* figured by Romer and Price (1940). The posterior parts of the blades are incomplete, but the anterior parts are fairly well preserved, and these show no indication of the flaring expansion seen in sphenacodonts and edaphosaurs. When these ilia were first extracted from the matrix, it was thought that they might belong to *Desmatodon hesperis,* but this seems highly unlikely because the neck is not constricted above the acetabulum as in *Diadectes,* and preparation revealed no sign of the external iliac shelf that is so prominent a feature in *Diadectes.* Fox and Bowman (1966) have argued convincingly that an external iliac shelf—indicating the presence of a considerable mass of axial musculature external to the upper part of the iliac blade—was not necessarily present in all of the most primitive reptiles. Nevertheless, the conspicuous presence of the external shelf in *Diadectes,* and also in the labyrinthodont *Seymouria* and the somewhat diadectid-like *Tseajaia* (Vaughn, 1964), as well as in the primitive captorhinomorph *Limnoscelis,* would seem to make it hazardous to postulate, on the basis of these two disarticulated ilia, such a major shift in pelvic morphology between Late Pennsylvanian and Early Permian diadectids—especially in view of Romer's (1956) reasons for regarding the external shelf as a primitive feature.

In the past, all Pennsylvanian ophiacodonts were almost automatically assigned to the genus *Clepsydrops,* but Romer (1961) has shown that Pennsylvanian ophiacodonts were probably quite diverse. The neural arch and, probably, the ilia described above may be identified as ophiacodont, but not more precisely at this time.

UCLA VP 1704, a small fragment from the anterior region of a right maxilla, suggests a sphenacodont. There are two teeth; the anterior one is 6 mm long, and the posterior is 11 mm long. Each tooth is somewhat flattened from side to side, is broad at the base, and tapers to a narrow tip. As in most sphenacodonts, and in contradistinction to other pelycosaurs (see Romer and Price, 1940), there is a "step" in the maxilla such that the ventral edge of this bone anterior to the first tooth lies at a conspicuously higher level than does the rest of the ventral edge. The first tooth arises partly from the region of the step—this resembles the general condition in *Dimetrodon.*

A number of parts of neural spines from Interval 300 represent a small edaphosaurian pelycosaur similar to one known in association with *Desmatodon hollandi.* Case (1908) set up the species *Naosaurus raymondi* on the basis of a fragment of neural spine—CM 1941—found at the Pitcairn site near Pittsburgh, in the middle of the Conemaugh Series, Pennsylvanian System. *Naosaurus* was later synonymized with *Edaphosaurus* (see Romer and Price, 1940). CM 1941 does seem definitely to represent a species of *Edaphosaurus,* in that it has the lateral tubercles so characteristic of that genus. This fragment

is about 12 mm long and is, as Case (1908:238) says, "oval in section with the greatest diameter antero-posterior." The greatest diameter is about 4 mm, and the least diameter, measured transversely at a "non-tubercular" level, is 3.4 mm. The collection from Interval 300 in the Sangre de Cristo Formation includes nine fragmentary neural spines closely comparable to CM 1941. In one of these, UCLA VP 1693, the greatest diameter is from side to side, but others are thicker from front to back. The transverse diameter taken between tubercles in UCLA VP 1693 is 3.3 mm. The shortest distance between two tubercles of a side in CM 1941 is about 4 mm, but this fragment is too short to give any idea of what variation may have existed; among the Sangre de Cristo spine fragments, which range in length up to 45 mm, the distance between two tubercles of a side varies from 2.5 to 15 mm. None of the tubercles is complete in CM 1941; in the Sangre de Cristo specimens they vary from about 1 to 5 mm in length. In some of the Sangre de Cristo spines the tubercles lie nearly opposite one another as in CM 1941, but in others the tubercles are staggered. Some show a longitudinal groove along one surface between the rows of tubercles.

The Sangre de Cristo spines are quite unlike those of the other known American Pennsylvanian species of *Edaphosaurus, E. ecordi* from the Garnett quarry in the Missouri Series in eastern Kansas (Peabody, 1957); the spine in *E. ecordi* is very much expanded from front to back in its upper portion, and the tubercles are only weakly developed. *E. raymondi,* as Romer and Price (1940) point out, is not easily separable on morphological grounds from the tiny *E. mirabilis* (Stephanian) and somewhat larger *E. credneri* (Lower Permian) of Europe. The Sangre de Cristo edaphosaur is best referred to as *Edaphosaurus* aff. *E. raymondi.*

Centra of the Sangre de Cristo edaphosaur have been difficult to recognize, but UCLA VP 1694 probably belongs to this form. This centrum has a broadly rounded ridge along the ventral midline in the style typical of *Edaphosaurus.* The posterior face of the centrum has a transverse diameter of 8.4 mm and a depth of 6.7 mm, but the fragmentary nature of the specimen makes other measurements unreliable, although it seems to have been about 11 mm long.

The presence of this edaphosaur at Interval 300 in the Sangre de Cristo Formation is of considerable interest in its association with *Desmatodon hesperis,* because the holotype of *E. raymondi* was found, at Pitcairn, in association with the holotype of *Desmatodon hollandi.* This supports the thesis of approximate equivalence in age of the Interval 300 site (probably Missouri Series) and the Pitcairn site (Conemaugh Series).

The presence of probably the three major kinds of pelycosaurs at Interval 300 is not surprising. All three, ophiacodont, sphenacodont and edaphosaur, are known from the Garnett quarry of Missourian age in Kansas (Peabody, 1957).

CONCLUDING REMARKS

Detailed comments on morphological peculiarities and the probable phylogenetic positions of the vertebrates known from Interval 300 have been made under the descriptions of the individual forms and will not be repeated here. The indications of age presented by the fossils may, however, be summarized.

The scales of palaeoniscoid fish are interesting as providing, along with the pelecypods, evidence for aquatic origin of the deposit, but they do not help in determination of age. Neither do the fragmentary remains of labyrinthodont amphibians help, although their presence does promise a future source, on an expanded geographic scale within North America, of greater knowledge of Late Pennsylvanian members of this group.

The new aistopod, *Coloraderpeton brilli,* does provide a definite indication of age. Aistopods, except for an Early Permian species of the apparently advanced genus *Phlegethontia,* are typically Carboniferous, and *Ophiderpeton,* the nearest known relative of *Coloraderpeton* as far as I can determine, is a Middle and Late Pennsylvanian genus (Baird, 1964). The evidence from the nature of the costal articulation in *Coloraderpeton* indicates that this genus is more primitive than *Ophiderpeton,* and this points to an age at least as old as Late Pennsylvanian.

The new species of the diadectid cotylosaur *Desmatodon, D. hesperis,* is certainly very close to *Desmatodon hollandi,* which is known only from the Conemaugh Series of the eastern United States. Detailed differences in dentition between these two species denote somewhat greater primitiveness for *D. hesperis,* but this seems not to be enough reason to postulate a great difference in age between the two; the conservative course is to regard them as approximately equal in age.

Edaphosaurus aff. *E. raymondi* provides corroboration of Late Pennsylvanian age, inasmuch as the holotype of *E. raymondi* was found in association with the holotype of *Desmatodon hollandi* about midway in the Conemaugh Series.

The fossils from Interval 300 thus provide strong evidence for assignment of at least the lower part of the Sangre de Cristo Formation in central Colorado to the Missouri Series, which is roughly the western equivalent of the Conemaugh Series. This fits perfectly the fact (Brill, 1952) that the Sangre de Cristo Formation in the Arkansas River valley of Colorado rests on rocks of Desmoinesian (Middle Pennsylvanian) age; and it makes it vastly preferable to accept Brill's (1952:822) alternative that "the lower part of the Sangre de Cristo formation in . . . Colorado is a nonmarine equivalent of . . . upper Pennsylvanian marine strata in northern New Mexico," rather than his tentative suggestion, based mostly on the quite natural misidentification of fragmentary *Desmatodon* remains as *Diadectes,* that the Upper Pennsylvanian of that region had been truncated by a pre-Wolfcampian erosional interval.

As already noted, the Sangre de Cristo site provides us with our first knowledge of Late Pennsylvanian North American tetrapods west of eastern Kansas. It may be hoped that this knowledge will be extended; there is promise of additional fossils from Interval 300, and further search of the Sangre de Cristo Formation in Colorado is needed. Further, the Sangre de Cristo fossils so far found, although hardly varied enough to be spoken of as a "fauna," do indicate that Late Pennsylvanian tetrapod faunas—in similar environments—were much alike throughout North America; and they will be important in considerations of the geographic distributions of Early Permian vertebrates (*e.g.*, Vaughn, 1966); that is, they provide evidence of "local" derivations of Early Permian faunas such as those of the Four Corners region.

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LITERATURE CITED

BAIRD, DONALD. 1964. The aïstopod amphibians surveyed. Breviora, (Harvard, Univ., Mus. Comp. Zool.) 206: 1-17.

BALTZ, E. H. 1965. Stratigraphy and history of Raton basin and notes on San Luis basin, Colorado-New Mexico. Amer. Assoc. Petrol. Geol., Bull., 49: 2041-2075.

BRILL, K. G., JR. 1952. Stratigraphy in the Permo-Pennsylvanian zeugogeosyncline of Colorado and northern New Mexico. Geol. Soc. Amer., Bull., 63: 809-880.

BYSTROW, A. P. 1939. Blutgefässystem der Labyrinthodonten (Gefässe des Kopfes). Acta Zool., 20: 125-155.

CARROLL, R. L. 1967. Labyrinthodonts from the Joggins Formation. J. Paleont., 41: 111-142.

CASE, E. C. 1908. Description of vertebrate fossils from the vicinity of Pittsburgh, Pennsylvania. Pittsburgh, Carnegie Mus., Ann., 4: 234-241.

———. 1911. A revision of the Cotylosauria of North America. Carnegie Inst. Washington, Publ. 145: 1-122.

FOX, R. C., AND M. C. BOWMAN. 1966. Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorphia). Univ. Kans. Paleont. Contrib., Vertebrata, 11: 1-79.

MCGINNIS, H. J. 1967. The osteology of *Phlegethontia,* a Carboniferous and Permian aïstopod amphibian. Univ. Calif. Publ. Geol. Sci., 71: 1-49.

OLSON, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. Fieldiana: Geol., 11(1): 1-53.

PEABODY, F. E. 1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. Univ. Kans. Paleont. Contrib., Vertebrata, 1: 1-41.

———. 1957. Pennsylvanian reptiles of Garnett, Kansas: edaphosaurs. J. Paleont., 31: 947-949.
ROMER, A. S. 1944. The Permian cotylosaur *Diadectes tenuitectus*. Amer. J. Sci., 242: 139-144.
———. 1947. Review of the Labyrinthodontia. Harvard, Univ., Mus. Comp. Zool., Bull., 99: 1-368.
———. 1952. Late Pennsylvanian and Early Permian vertebrates of the Pittsburgh-West Virginia region. Pittsburgh, Carnegie Mus., Ann., 33: 47-113.
———. 1956. Osteology of the Reptiles. Univ. Chicago Press, 772 pp.
———. 1960. The vertebrate fauna of the New Mexico Permian. New Mexico Geol. Soc. Guidebook of Rio Chama Country, 11th Field Conf., p. 48-54.
———. 1961. A large ophiacodont pelycosaur from the Pennsylvanian of the Pittsburgh region. Breviora (Harvard, Univ., Mus. Comp. Zool.), 144: 1-7.
———. 1964. *Diadectes* an amphibian? Copeia, 1964: 718-719.
———, and L. I. PRICE. 1940. Review of the Pelycosauria. Geol. Soc. Amer., Spec. Paper 28: 1-538.
VAUGHN, P. P. 1964. Vertebrates from the Organ Rock Shale of the Cutler Group, Permian of Monument Valley and vicinity, Utah and Arizona. J. Paleont., 38: 567-583.
———. 1966. Comparison of the Early Permian vertebrate faunas of the Four Corners region and north-central Texas. Los Angeles County Mus. Nat. Hist., Contrib. in Sci., 105: 1-13.
WELLES, S. P. 1941. The mandible of a diadectid cotylosaur. Univ. Calif. Publ. Geol. Sci., 25: 423-432.
WHITE, T. E. 1939. Osteology of *Seymouria baylorensis* Broili. Harvard, Univ., Mus. Comp. Zool., Bull., 85: 325-403.

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